

# The effect of audience on intrasexual interaction in the male fiddler crab, *Uca maracoani* (Latreille 1802–1803, Decapoda, Ocypodidae)

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Received: 18 December 2015 / Accepted: 7 September 2016 / Published online: 21 September 2016  
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**Abstract** Animal communication occurring in wide networks can involve signals sent to several receivers. The animals composing the audience may affect how individuals display during an interaction and may change the message that is sent. In this study, we investigated whether the presence of a conspecific affected the intensity of agonistic interaction between male fiddler crabs, *Uca maracoani*. Pairs of males of the same size were observed when in the presence of a male, a female or no crab as audience. We found that if there is a female audience, males became more aggressive and interacted the most. Also, the female audience leads to an increase in incidence of male foaming, possibly indicating predisposition for mating. If the audience was a male or if there was no audience, there was no significant difference in interaction. These results indicate that the presence of an audience affects the way male fiddler crabs interact and the type of displays they show. Therefore, the context seems to guide the fiddler crab behavior in terms of how they perform in order to send information about themselves to conspecifics.

**Keywords** Interaction · Aggression · Audience · Communication · Fiddler crab

## Introduction

Communication is the exchange of information between at least two individuals. This can include visual signals, sounds, smells, electrical or even physical interactions between those involved in sending and receiving the messages (Dzieweczynski et al. 2012). An animal uses information received to recognize mates, distinguish conspecifics from heterospecifics or avoid predators; valuable abilities for survival and reproduction. Processing signals from other animals in order to properly respond is an adaptive feature (McGregor and Peake 2000). However, information exchanged by the sender and receiver can also reach individuals that are not directly involved, namely the spectators or audience (Doutrelant and McGregor 2000). These individuals participate in forming the network in question and may affect the type of information being sent (McGregor 2005).

Signaling may be affected by other animals directly interacting with the sender (Doutrelant et al. 2001) or the presence of animals not directly involved in the interaction (Doutrelant and McGregor 2000). The audience gathers information from conspecifics (Herb et al. 2003) in order to evaluate their potential to defend resources (McGregor and Peake 2000). Nevertheless, the audience presence may affect the type of signals sent (Semple et al. 2009), and thus involves additional costs and/or benefits for the signalers (Matos and McGregor 2002). For example, the common whitethroat (*Sylvia communis*) female attracts more than one male during the courtship phase so as to trigger competition and choose the best mate by observing their fight performance (Balsby and Dabelsteen 2003a, b), and the male Siamese fighting fish (*Betta splendens*) changes fighting patterns against other males when a female is observing, to show his mating potential (Doutrelant et al.

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2001). In vertebrates, a number of studies have shown the effects of an observer on the type of signals emitted by fighters (Dugatkin 2001; Earley and Dugatkin 2002; Matos et al. 2003; Matessi et al. 2010).

Among invertebrates, although cognition is more restricted due to a generally smaller nervous system than those of vertebrates (Giurfa 2013), they possess behavioral and cognitive repertoires comparable to animals with big brains (Perry et al. 2013). For instance, bees are able to categorize signals (Zhang et al. 2004), crickets were shown to learn by observing conspecifics' behavior (Giurfa and Menzel 2013), and crabs can recognize conspecifics and their sex, establish/defend territories and choose mates based on certain features (Detto et al. 2006; Booksmythe et al. 2010). However, whether a conspecific observer can be recognized and whether this affects an interaction has yet to be investigated.

Fiddler crabs are good models for territoriality and agonistic encounter studies (Booksmythe et al. 2010; Detto et al. 2010; Muramatsu and Koga 2016). They are semi-terrestrial animals that hold territories around a burrow, essential for survival during high tides in their intertidal habitats (Crane 1975). They maintain social relationships with neighbors and show a rich agonistic behavioral repertoire (Pope 2000), comprising varied acts of aggression (threats, chasing, escalated fights). This is more pronounced in males that are sexually dimorphic, characterized by an enlarged claw (Crane 1975), which is used both in intra- and intersexual interactions to delimit territory and burrows, control other crabs' access to its resources (food, territory, mate), and attract females (Klaassen and Ens 1993; Murai and Backwell 2006; Mautz et al. 2011). During intrasexual interactions, male fiddler crabs first wave their claw to show their size and power (Booksmythe et al. 2010; Santos et al. 2015). Then, more aggressive interactions ensue, including touching and pulling the opponent's claw, intertwining and holding claws, and suspending and pushing the other animal (Santos et al. 2015), behaviors that signal their defense potential and determine the distribution of resources.

However, due to the high energy cost of fights (Rovero et al. 2000) and the conspicuity of waving to predators (Jordão and Oliveira 2001), fiddler crabs adjust their waving rate according to male competition in order to increase mate attraction and decrease energy expenditure in agonistic interactions (Milner et al. 2012). In this context, other crabs may gather information from waving and fighting as signs of one's potential to defend resources and mate. In fact, Milner et al. (2010) suggest that male fiddler crabs copy other males' claw waving even when they cannot properly see the female, indicating that signals are perceived and affect each other's waving behavior. Therefore, we intended to test whether agonistic encounters

between males are affected by the presence of a female or a male audience, in order to determine fiddler crab perception and response to conspecifics.

In tropical zones, ovigerous female fiddler crabs are found throughout the year due to the stability of abiotic variables (Cobo 2002). *Uca maracoani* is a narrow-front fiddler crab species (Masunari 2006) occurring in the coastal region from Venezuela to southern Brazil (Melo 1996), in the intertidal and mudflat areas (Hirose and Negreiros-Fransozo 2008). This species preferentially adopts the surface mating strategy (Negreiros-Fransozo, personal communication), in which mating occurs near the female's burrow. In this type of mating system, males search for females and engage in aggressive encounters with other male competitors to guarantee its reproductive success. Since communicating its potential as competitor and reproducer may favor the fiddler crab's success in fights, the aim of the present study was to test whether the presence of a male or female audience changes the way two *Uca maracoani* males interact. For this, we observed the behavior of pairs of *U. maracoani* males when a female was chosen to be the audience, when a male was chosen to be the audience, and when no audience was present.

## Materials and methods

The study was conducted from July to September 2013 in the Ceará-Mirim River estuary, located in the city of Extremoz, Rio Grande do Norte State (05°40'32.25"S; 35°14'19.61"W). The Ceará-Mirim River mangrove covers 17,000 m<sup>2</sup>, average temperature is 26.1 °C and annual relative humidity 77 % (IDEMA 2008). The mangrove area belongs to the Centro Tecnológico de Aquicultura (CTA) of Universidade Federal do Rio Grande do Norte (UFRN). The wet area of the mangrove forest (close to the river and containing mainly mud soil) is only occupied by *U. maracoani* (Latreille, 1802–1803), which spend most of their time feeding and interacting with conspecifics.

In the present study, we used 96 specimens of *U. maracoani*: 12 males and 12 females as audience, and 72 males (36 pairs) divided into three experimental groups. These groups consisted of (1) a female audience: 12 pairs of *U. maracoani* males were observed when a female was chosen to be the audience, (2) male audience: 12 pairs of *U. maracoani* males were observed when a male was chosen to be the audience, and (3) no audience: 12 pairs of *U. maracoani* males were observed without any audience. For every male pair + audience crab, the animals collected had similar body size (Table 1).

For the tests, we positioned a plastic box (50 × 30 × 26 cm, length × width × height) in the mangrove forest area occupied mainly by *U. maracoani*

**Table 1** Experimental two male *Uca maracoani* body features (mean ± SD) in each condition

Features (cm)	Condition		
	Female observer ( <i>n</i> = 12)	Male observer ( <i>n</i> = 12)	No observer ( <i>n</i> = 12)
Male–male carapace length	2.73 ± 0.22 and 2.46 ± 0.29	2.63 ± 0.33 and 2.64 ± 0.37	3.05 ± 0.49 and 2.82 ± 0.56
Male–male carapace width	2.28 ± 0.28 and 2.10 ± 0.20	2.10 ± 0.30 and 2.07 ± 0.27	2.53 ± 0.59 and 2.40 ± 0.58
Male–male claw length	4.35 ± 0.75 and 4.15 ± 0.75	4.13 ± 0.72 and 4.14 ± 0.93	3.97 ± 0.43 and 3.72 ± 0.50
Observer carapace length	2.13 ± 0.33	2.76 ± 0.47	–
Observer carapace width	1.78 ± 0.29	2.16 ± 0.42	–
Observer claw length	–	4.02 ± 0.68	–

and filled half the box with local mud. A glass partition was introduced into the box, dividing it into two areas: a smaller side for the observer (10 × 30 cm) and a larger arena for the male–male encounter (40 × 30 cm) (Fig. 1). Behavior was tested during the light phase and low spring tides (between 9 a.m. and 3 p.m.) when fiddler crabs are more active. We manually collected two males with similar carapace and claw size and placed them in the larger side of the arena (crab body sizes are shown in Table 1). Next, another *U. maracoani* (female or male audience) was

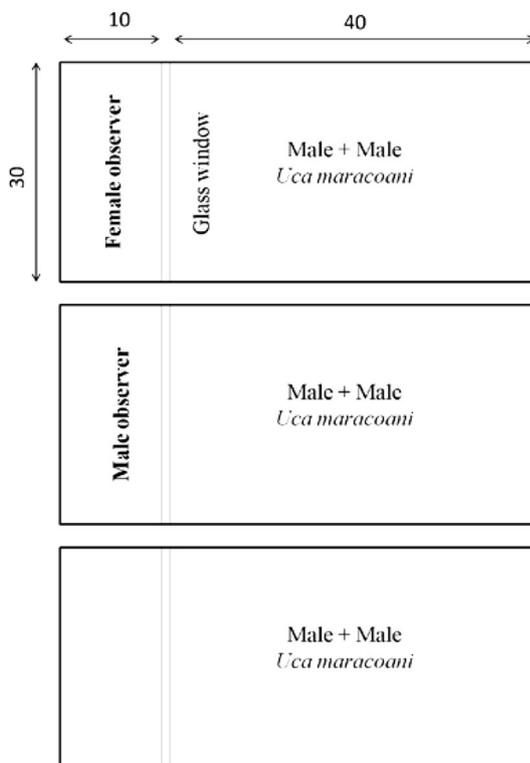
introduced into the smaller area of the box. A glass window between the males and the audience allowed animals to make visual but not physical contact. Animals were left to acclimate for 3 min in the experimental box and behavior was then recorded for 10 min using a camcorder (Sony DCR-SX45 Digital Video Camera Recorder) connected to a 2-m tripod. After the 10-min interaction period, the 3 animals (audience + male pair) were removed from the box and left 4 m from the experimental area, in order to avoid re-sampling the animals.

After each behavioral recording, the window was cleaned, the mud base rebuilt and a new pair of males + a new audience crab placed in the box. To randomize data collection, one sample (audience + pair) from each experimental group (female audience, male audience and no audience) was recorded at a time, in sequence.

We recorded the number of agonistic signals, interactions displayed and distance between animals in *U. maracoani* males during the 10-min recording. The scale of signaling/interaction was classified into four levels, as modified from Pope (2000) and Mansfield (2009): type 1—threat wave (signaling), type 2—major claw touch, type 3—major claw intertwining, and type 4—hold, suspend and push the other animal (2, 3 and 4: agonistic interactions). The arena was divided into 2-cm squares, drawn on the front of the computer screen so that the position of the crabs could be recorded every 10 s and then plotted on an *x–y* axis. Six points were collected for each minute.

The mean position of each male produced the barycentric coordinate for each 1-min period. We measured the distance between crabs every 10 s, followed by the mean distance between them and between each male and the window. We also recorded the number and type of signal/interaction displayed by the two males.

During data collection, we observed that some of the male pairs were producing foam. Although this was not an expected behavior, we video recorded and analyzed male foaming in each experimental treatment. There are only two references regarding *Ucides cordatus* foaming behavior related to mating (Nascimento 1993; Wunderlich et al. 2008). While this behavior has not been observed in any



**Fig. 1** Schematic set-up of the conditions tested: two male *U. maracoani* were allowed to interact in the bigger arena either in the presence of a conspecific female, a conspecific male or no observer. The numbers show the dimensions of the box in cm. The walls of the box were 26 cm tall and it was filled to a depth of 13 cm with mangrove mud. The observer and the male + male areas were divided by a transparent glass window

other crab species or reported scientifically, we noted the occurrence of foaming in *U. maracoani* during male intrasexual interaction.

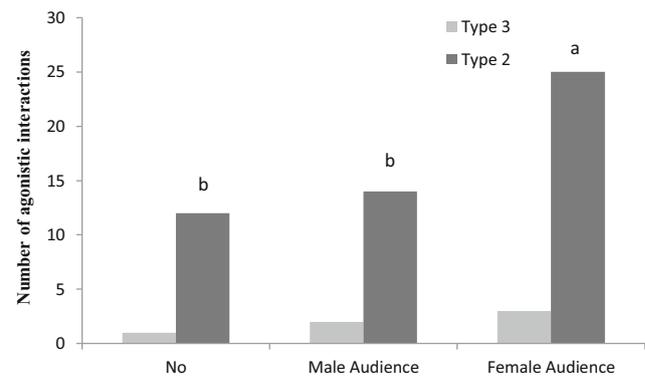
Sample size was tested using G-Power software and showed that for  $n = 12$ , the size effect equals 0.5, the  $\alpha$  probability error equals 0.05 and the test power equals 0.72, thus showing  $n = 12$  is sufficiently strong. All data were analyzed for normality [Shapiro–Wilk univariate test (Shapiro and Wilk 1965)] and homoscedasticity [Brown–Forsythe univariate test (Brown and Forsythe 1974)]. Parametric tests were used in cases of normal and homoscedastic data; otherwise, we used nonparametric equivalence tests. The one-way ANOVA test was used to compare the mean distance between crabs and from the window, and the Kruskal–Wallis test to compare carapace size. The Kruskal–Wallis test was also used to compare the number of agonistic interactions displayed and foaming frequency among the conditions. The Student–Newman–Keuls post hoc test was also applied. To compare distance, signaling/interaction and foaming between treatments, we performed permutational multivariate analysis of variance (PERMANOVA), with permutation ( $n = 9999$ ) and the euclidean distance measurement.

The matrix data were z-score transformed, followed by one-way PERMANOVA. Next, we applied the betadisper function of the “vegan” package (Oksanen et al. 2013) to test the homogeneity premise. The Bray–Curtis dissimilarity index matrix was used, and statistical analyses were performed using R software (R Development Core Team 2015), considering  $\alpha = 0.05$  (Zar 2010). Pairwise comparisons (Bonferroni-corrected  $p$  values) for the PERMANOVA posteriori test were performed using the PAST program (Hammer et al. 2001).

## Results

The animals had similar carapace size (Kruskal–Wallis,  $H = 2.97$ ,  $p = 0.23$ ) (Table 1). From the scale of signaling/interaction used in this study, we did not observe type 1 (wave) or type 4 (hold, suspend and push the other animal) during male–male encounters. However, interaction type 2 (major claw touch) occurred in all treatments and was statistically higher in male pairs with female audience than in the other treatments (Kruskal–Wallis,  $H = 8.70$ ,  $p = 0.013$ ). While type 3 interactions (major claw interlace) occurred in all treatments, it was not statistically different (Kruskal–Wallis,  $H = 2.60$ ,  $p = 0.27$ ). The total number of interactions was also higher in the male pairs with female audience than in other pairs (Kruskal–Wallis,  $H = 9.77$ ,  $p = 0.008$ ) (Fig. 2; Table 2).

The comparison between distances maintained from males during the agonistic encounters showed no



**Fig. 2** Total number of agonistic interactions observed from a male–male *Uca maracoani* contest in which there were no observers ( $n = 12$ ), a male observer ( $n = 12$ ), or a female observer ( $n = 12$ ). Type 2 interactions (claw touch) were significantly higher in the presence of a female observer (Kruskal–Wallis,  $p < 0.05$ ). Type 3 interactions (major claw interlace) did not differ among conditions (Kruskal–Wallis,  $p > 0.05$ ). The total number of interactions (type 2 + type 3) was also higher in the presence of the female audience (Kruskal–Wallis,  $p < 0.05$ ). Different lower case letters indicate statistical difference (Kruskal–Wallis,  $p < 0.05$ )

differences (one-way ANOVA,  $F = 0.10$ ,  $p = 0.90$ ), and the distance from the males to the glass window was also non-significant (one-way ANOVA,  $F = 1.97$ ,  $p = 0.157$ ) (Table 2).

Foaming frequency was significantly higher in males with female audience, while pairs of males with male audience or no audience did not differ (Kruskal–Wallis,  $H = 6.78$ ,  $p = 0.034$ ) (Table 2).

The data matrix of distance, signaling/interaction and foaming between treatments obtained homogeneity of multivariate dispersions (permutation test for homogeneity of multivariate dispersions:  $F_{2,33} = 3.46$ ,  $p = 0.056$ ). PERMANOVA analysis showed statistical differences between treatments ( $F = 2.99$ ,  $p = 0.002$ ). According to pairwise comparisons, male pairs with female audience were statistically different from those with male audience ( $F = 3.23$ ,  $p = 0.03$ ) and no audience ( $F = 4.73$ ,  $p = 0.001$ ). There was no statistical difference between male audience and no audience ( $F = 0.18$ ,  $p = 1.00$ ). MDS analysis indicated that female audience was different from males and no audience. These differences can be explained by the frequency of type 2 and 3 interactions, and foaming when a female was the audience (Fig. 3).

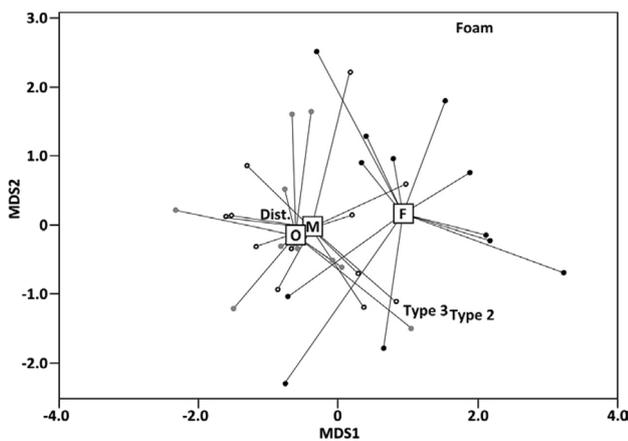
## Discussion

We found that agonistic interaction increased in *Uca maracoani* males in the presence of a female, but did not change when a male was present. The female audience not only increased the number of major claw touches between

**Table 2** Male–male *U. maracoani* behavior in the presence/absence of an observer

Behavior	Female observer ( <i>n</i> = 12)	Male observer ( <i>n</i> = 12)	No observer ( <i>n</i> = 12)	<i>p</i>
Male–male distance to each other (cm) (mean ± SD)	4.1 ± 1.12	4.2 ± 0.96	4.3 ± 0.95	0.90
Male–male distance to glass window (cm) (mean ± SD)	4.5 ± 1.33	5.2 ± 1.27	4.2 ± 1.53	0.16
Number of major claw touch	27 <sup>a</sup>	14 <sup>b</sup>	12 <sup>b</sup>	0.013
Number of major claw interlace	5	2	1	0.27
Number of hold, suspend and push	0	0	0	–
Total number of interactions	32 <sup>a</sup>	16 <sup>b</sup>	13 <sup>b</sup>	0.008
Foam frequency (%)	75 <sup>a</sup>	33 <sup>b</sup>	25 <sup>b</sup>	0.034

Lowercase letters indicate statistical differences between treatments



**Fig. 3** Ordination of *Uca maracoani* males' behavior sets. The metric multidimensional scaling plot shows differences between groups (*F* female audience, *M* male audience, *O* no audience) and respective behavioral parameters (*Dist.* distances between animals, *Type 2* and *Type 3*, and *Foam* agonistic interaction). The *square shapes* represent the centroid distance between groups

males, but also raised male foam production, possibly indicating the male's aptitude to copulate. Thus, it seems that the audience effect on male agonistic interaction is biased by the presence of a female. Although our results reinforce the idea of audience effect in fiddler crab interactions, as suggested by Milner et al. (2010), we propose that this effect is restricted to the female presence. Additionally, this study is the first to show foaming related to agonistic interaction in male fiddler crabs, indicating that foam can be used as a signal during agonistic displays.

We found that pairs of males in the presence of a male audience or with no crab as audience showed similar behavioral patterns (Fig. 2). A number of theories can be put forth to explain the absence of a male audience effect. In other fiddler crab species interactions increase when faced with other males in order to establish a residence to attract females (Pope 2000; Santos et al. 2015). However, the opposite was observed in our study with *U. maracoani*. In this species, males that have established a territory engage in aggressive battles to guarantee possession of the area when

the female is present, but when there is no territory settled and no female audience, there is also no resource that warrants fighting for. Female *U. maracoani* seem to be the main resource when there is no established territory to defend. In *U. annulipes*, Milner et al. (2012) observed that males adjust their waving rate according to the number of male neighbors, indicating their perception of the female as a potential mate and their immediate level of competition. This finding suggests females are a more important resource, and although territory establishment contributes to aggressive encounters, it is still a secondary concern. Thus, the absence of a female may have removed the reason for fighting.

Moreover, interacting males and the observer had the same carapace and claw widths. Size has already been shown to be a decisive factor in fiddler crabs winning or losing a battle (Jaroensutasinee and Jaroensutasinee 2003; Bolton et al. 2013). According to Bolton et al. (2013), individuals assess each other's resource-holding potential (RHP, i.e., power, size, residency, burrow ownership, etc.; Parker 1974) to decide how they would invest in fighting (whether to start a fight, for how long, when to desert). Similar RHPs make assessment difficult, and combatants continue to fight to gain information about their rivals (Jennions and Backwell 1996; Bolton et al. 2013). In contrast, differences in RHP favor stronger individuals (high RHP: residency, large claw) and duration of the agonistic encounters are usually shorter (Jennions and Backwell 1996). Here, we did not observe rivals' RHP assessment, and closely matched RHP was expected throughout our treatments (types of audience). Thus, RHP may not have affected male–male interactions but the type of audience seems to influence the males' behavior.

Another explanation for the low effects of male audience would be that male fiddler crabs do not change their display because they use honest signaling. According to Gavassa et al. (2013), signal reliability is maintained by the costs involved in communicating. Thus, when signals have low costs, animals cheat without high risk, but when signals have high energy costs, the likelihood of dishonesty decreases (Akçay et al. 2013). In the case of fiddler crabs,

since interaction types 2, 3 and 4 (see “[Materials and methods](#)” section) are highly costly (Bookmythe et al. 2010), honest signaling is more frequently observed. Similar results of low-cost behavior absence were obtained by Jennions and Backwell (1996) for *U. annulipes*. These authors found that male encounters already began with costly behaviors and fighting ability assessment may occur on the basis of size before the beginning of physical interaction.

In contrast to what was observed in the presence of a male audience, the female audience changed the way in which two males interacted (Fig. 2). Although there were no displays toward the female, the number of interactions between the two males increased significantly with a female audience. The fact that neither male had its own territory may have contributed to this response.

It is well established that narrow-front fiddler crabs exhibit a surface mating system while their broad-fronted counterparts use a burrow-mating strategy. Some fiddler crabs, however, alternate between both strategies while others have yet to be fully described (deRivera and Vehrencamp 2001). *U. maracoani* is a narrow-front species (Rosenberg 2001) that seems to use the surface strategy (Negreiros-Fransozo, personal communication). In species adopting this strategy, mating occurs close to the female’s burrow, since they have a small brood and do not need special enclosed areas to protect their eggs (Christy and Salmon 1984). These crabs do not aggressively compete for burrows in order to attract females, since females build and defend their own burrows, but males wave vigorously in the presence of females to draw potential mates’ attention (deRivera and Vehrencamp 2001; Christy and Salmon 1984).

Increased signaling towards the female seems to be proportional to male competition (Weir et al. 2011). In the red crayfish, (*Procambarus clarkii*), Aquiloni and Gherardi (2010) observed that the female chose male mates based on the latter’s potential to win a fight and ability to defend its territory, feeding area and females. For these animals, the visual observation of conspecifics contributes to better mate assessment (Atema and Cobb 1980). For male fiddler crabs, the ability to use their claw during agonistic encounters is a good sign of power and motivation (Andersson 1994), and females may use this signal to evaluate them. Signals that mediate animal communication contain valuable information about fighting capacity, which may have important consequences for the female’s choice (Thorpe and Griffin 1962). In this sense, balancing the information sent in the presence of observers may involve either costs (confrontation) or benefits (mate attraction) for the sender, depending on who the receiver is.

In our study, we did not observe waving, which may indicate that males were not signaling to the female. Thus,

the males’ first intention could have been to establish a combat winner to attract the female. Other animal species have been shown to increase the number of agonistic interactions between males, which serve both to scare away other males and to show mating potential to females (Doutrelant et al. 2001).

A final point to discuss is foam production by males in the presence of a female (Table 2). Other studies have reported foam production in crabs: Wunderlich et al. (2008) and Nascimento (1993) observed that *Ucides cordatus* foaming occurs before copulation and was suggested to be related to female attraction. While foam production was not expected in our study, we observed differences in this type of behavior between groups, suggesting that the presence of females stimulates male foaming. However, a better understanding of foam production and its association with the male–female relationship deserves more attention.

The data obtained allow us to suggest that a female audience affects male–male interaction by increasing male investment in fighting and indirectly sending information to a potential mate (the female). Thus, the presence of a female seems to determine how males interact in agonistic encounters. Since females are an important resource in guaranteeing reproductive success, males increase energy expenditure while fighting. Hence, males may alter their interaction strategy in order to have access to this important resource (female). On the other hand, the male audience may not be a sufficient motivator for agonistic interaction. Our results suggest that male *U. maracoani* can distinguish between audience types and adjust their behavior accordingly. This behavior allows males’ access to the main resource providing reproductive success by showing better territorial defense abilities. Thus, intersexual recognition and the ability to properly interact in a male–male encounter contribute to the balance between agonistic interaction costs and mate acquisition benefits. Future studies investigating the female preference for winners or losers of a fight against males that did not interact, and preference for males holding territories against males without territories may contribute to better understanding the audience effects in fiddler crabs.

**Acknowledgments** We thank Ms. Vanessa B. Guerra, Jéssica J. Oliveira and Mr. Sávio A.S.N. Moraes very much for assistance with collection. We thank the anonymous reviewer for helpful comments and constructive criticism.

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